SYSTEMATIC, NATURAL HISTORY, AND ZOOGEOGRAPHIC NOTES ON THE GENUS *AGRA* FABRICIUS, WITH A DESCRIPTION OF A NEW SPECIES FROM PANAMA (COLEOPTERA:CARABIDAE:LEBIINI)

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Abstract

A new species, *Agra lavernae* Erwin, from Cerro Campana, Panama is described and illustrated. *Agra* species are numerous in the Neotropical region yet very few specimens have been collected. Most papers previously published did not provide keys or syntheses. A trend curve shows that taxonomy on the group was done in plateaus. Past classification placed *Agra* and its sister group *Agridia* in the tribe Agrini, but here the two are regarded as Lebiini because of defense mechanism structure. *Agra* species are forest canopy specialists, but their food, oviposition habits, and behavior are unknown. Sexual dimorphisms in *Agra* species are numerous.

The purposes of this paper are to set forth objectives of my long term *Agra* study, provide some information for collectors, encourage loan of material, and make known a new species from Panama in need of a name for another publication. The species described here was used as an example of specialized adaptive form (Erwin, in press b).

Surely the most elegant and graceful group of neotropical carabid beetles yet discovered is that of *Agra*. These elongate, often metallic, "long-necked" beetles have gladdened the heart of many 'black lighters' on warm and humid tropical nights. Usually, however, only one or two specimens will arrive at the light during a good night, creating one of the major problems with *Agra* studies; that is, very little material has been accumulated over the past 200 years. Most species are represented by few specimens (although there are exceptions), there are hundreds of species, mostly undescribed, and most species seem to be quite local in distribution. I began gathering specimens for a revision in 1973, borrowing the holdings of most major museums in North America (and São Paulo, Brazil)—a mere 1650 specimens, but representing 312 species, ca. 30% of which are represented by a single specimen. This material is being gathered for three reasons: 1) to provide study material for a generic revision; 2) to provide a phylogenetic and geographic picture of the genus in order to test the neotropical forest refugium hypothesis set forth by Haffer (1969), Vanzolini (1970), and others; and 3) to determine the sister group of the genus in order to aid a reclassification of the "truncatipennes" (Erwin, in press a, in press b, MS).

Systematics

Thus far the nomenclatorial history of *Agra* has been that of single species descriptions or multiple descriptions. There have been no syntheses

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nor keys to species that are reliable. In recent years S. L. Straneo described about 100 new taxa and Van Dyke (1943) described a single new taxon from Mexico. Otherwise, the literature of the 19th century must be consulted (cf. Bates, Brullé, Buquet, Chaudoir, Chevrolat, Dejean, Fabricius, Gory, Guerin, Klug, Lansberge, Liebke, Lucas, Olivier, Putzeys, Steinheil, and Thomson). A "trend curve" (Steyskal 1965) is provided (Figure 1) which shows that, contrary to trend curve theory, work in some groups is done in plateaus and projections of numbers of taxa is impossible from any point on the curve. This will be especially true of tropical forest canopy groups which require special collecting techniques. If the *Agra* trend curve was smoothed and inverted (White 1975), it predicts the genus has, at a minimum, about 2000 species. I doubt this, but predict about 1000 species based on the material I have studied thus far.

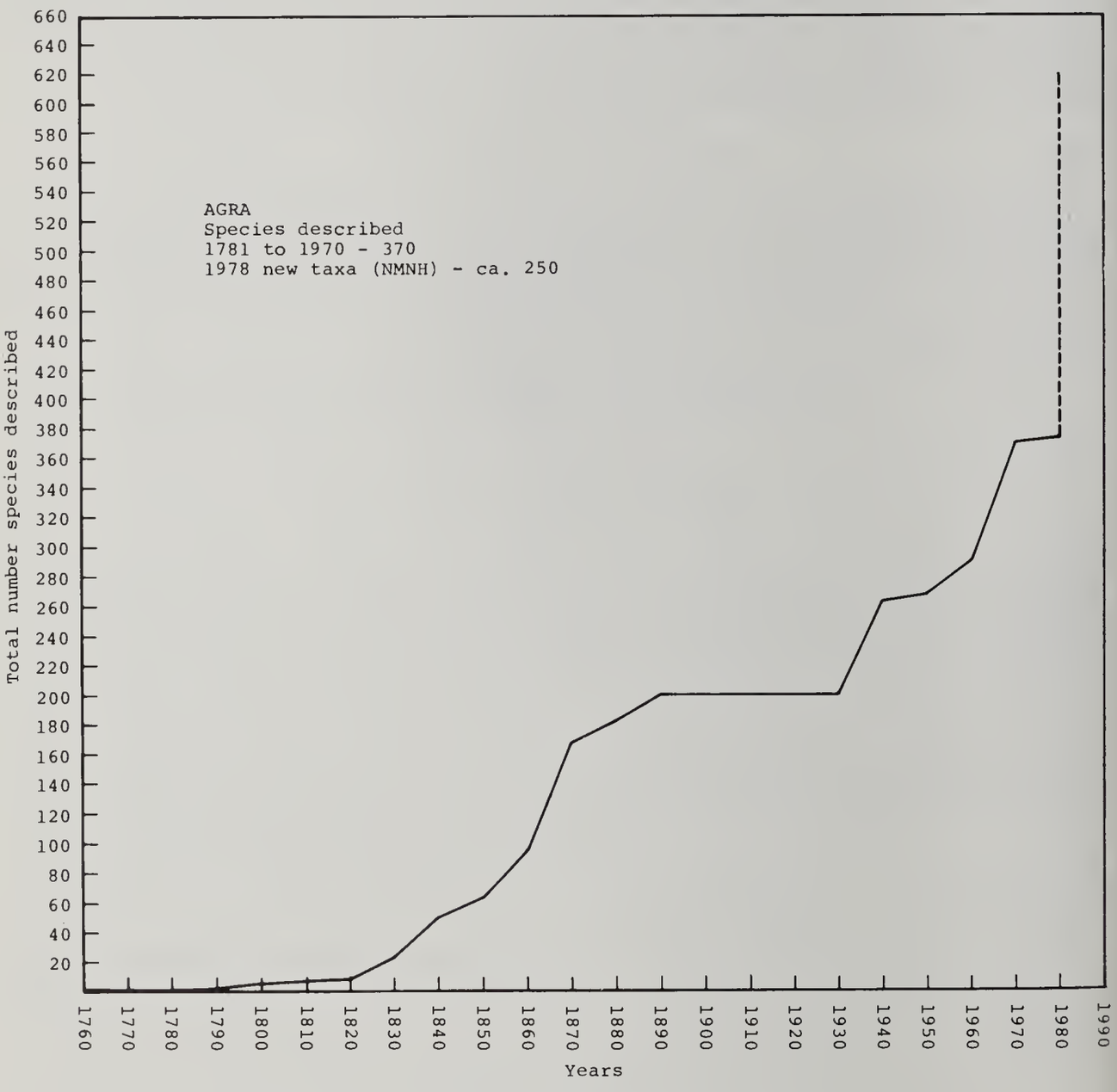

Figure 1. Trend curve for species of *Agra*.

Horn (1881) noted similarity of ligula structure among *Agra,* Odacanthini, and Ctenodactylini members, pointing out that *Agra* species classified as "Lebiide" would "introduce confusion as great as [doing the same]

with *Mormolyce."* As he did with the latter group, Horn erected a new tribe for both *Agra* and *Agridia* to be placed near the Odacanthini and Ctenodactylini. Bates (1883) regarded *Agra* and *Agridia* as subfamily Agrinae. The group thus has been regarded as a subfamily or more often tribe since Horn. Unfortunately Horn was misled by the elongate form of *Agra,* Odacanthini, Ctenodactylini, and *Mormolyce,* and he ignored many technical details which help to place *Agra* properly in carabid classification. Among other things, the structure of the defense mechanism of *Agra* members is clearly synapotypic with the Lebiomorphi and I regard *Agra* and *Agridia* as Lebiini (Erwin, in press b). The question of whether or not *Agridia* is a good genus awaits analysis and revision.

Natural History

Agra species are adapted to life in the forest canopy and are seldom found within easy reach of the average collector except at black light. Occasionally, single individuals are obtained by sweeping wilted leaves or broken limbs on downed trees, usually at ecotonal areas (Figure 2). These canopy species probably follow the "canopy" down in the transition zone (Figure 2) much as some tree top birds do (G. Morton, personal communication). These areas should always be carefully swept for canopy carabids and observations made on surrounding forest types to determine source areas. In the canopy, *Agra* members probably spend much time running the surfaces of leaves. Although not observed directly, I judge this leaf running to be their activity based on the nature of tarsal vestiture (Figure 3).

Other beetle groups with similar vestiture (*Calleida, Lebia, Calophaena,* Chrysomelidae, etc.) were observed to run on leaves, and *Agra* was repeatedly collected in rolled or wilted leaves in ecotonal areas. Individuals I observed on Barro Colorado Island, caged inside a large terrarium, spent equal time on leaves and twigs.

Figure 3. Anterior tarsomeres (×65) and modified setae (×700), ventral aspect of *Agra darlingtoni,* Barro Colorado Island, Canal Zone, Panama.

Some members of *Agra* were collected by diurnal sweeping but most specimens were collected at night at lights. I suspect these beetles are primarily nocturnal in habits and merely hide during the day in rolled and wilted leaves. During the dry season in various parts of Mexico, G. E. Ball and D. R. Whitehead found several species of *Agra* in epiphytic bromeliads but, again, only sporadically and in very low numbers (Whitehead, personal communication).

Agra species of lowland humid forest canopies are the top predator among beetles in terms of size (Erwin and Scott, in preparation). The question remains 'predators of what?'. There seems to be a correlation of axinoform palpi and snail predation in carabid beetles (Erwin, in press b). All *Agra* species have the labial palps strongly axinoform. It is possible that tree snail predation is their speciality, and perhaps this accounts for their incredible diversity in the neotropical forest canopy. Tree snails are quite diverse there too. Additional evidence for this snail eating hypothesis is the elongate nature of their forebody structures—prothorax, head, and mouthparts—which might aid in gleaning inside the shell (as in Cychrini).

Sexual dimorphism in *Agra* members is exhibited in more characteristics than in other carabids. This phenomenon is amply demonstrated in some or all species in the following characteristics: Head shape—various, often male square, female ovoid; front femur—male robust, female normal for carabids; ventral vestiture—male variously and amply hirsute, female sparsely or differently hirsute or sparsely setiferous; sternum VI—various differences in shape, vestiture, punctation always present; build—male robust, female slight; palpi—labial terminal article large in males.

Agra female members have the most bizarre ovipositor of the Carabidae. The styli are located quite close together, usually heavily sclerotized and

elongate, and each has two spinose setae apically. These are located at the end of a greatly extensible tube, which, when everted, is equal in length to 1/2 to 2/3 the body length. No other carabid I know of has anything remotely similar to either the styli or the tube. The delicate nature of the tube indicates to me that the ovipositional substrate is not penetrated by much force if any. I suggest that leaf axils, existing insect burrows, or organic debris in tree holes or crotches are possible sites. A more intriguing possibility is oviposition deep inside the shell of a living tree snail with the resultant larva being an ectoparasitoid; it is possible that both adults and larvae consume the same food, given the usual abundance of tree snails. Ectoparasitoidism is already known among the Lebiini (Erwin and Erwin 1976; Erwin, in press c).

The only clue to exact canopy habitat is the northern limit of the range of the genus. Two species were collected on the Esperanza Ranch near Brownsville, Texas. The only tropical "canopy elements" there are found in a grove of palms. This clue may indicate that some or all *Agra* members have something to do with tropical palms. Neotropical palms have not been investigated for carabid associations, but I suggest it would be a rewarding study.

Measurements

For studies of *Agra* members I adopted the following measurements and abbreviations:

Head: *Total length* (TLH)—anterior labral edge to back of head capsule where it joins the neck; *Total width* (TWH)—width across head capsule at hind edge of eye; *Total depth* (TDH)—depth of head capsule at hind edge of eye; *Eyes* (HE)—width across eyes; *Interocular distance* (ID)—head capsule between eyes; *Frons width* (MFW)—maximum distance across frons at front edge of eyes (excluding antennal base); *Frons/labrum length* (LBE)—anterior margin of labrum to posterior frons along midline at hind edge of eye; *Clypeus/labrum length* (LFE)—anterior margin of labrum to hind edge of clypeus or frons along midline at anterior margin of eye.

Prothorax: *Prothorax length* (PL)—total length of pronotum along midline; *Prothorax width* (PW)—total width of prothorax at widest point.

Standardized body length (Ball 1972) is given.

Agra lavernae Erwin, **new species**
(Figure 4)

Type-specimen: Holotype female in USNM, type number 75854, USNM ADP number 33343.

Type-locality: Cerro Campana, 850 m, Panama Province, Republic of Panama, 8° 40′ N, 79° 56′ W. 29 March 72, B. Bivin Collector.

Diagnosis: The elegance of members of this small species makes it easily recognized; small size, ferruginous head and pronotum, metallic green elytral base, testaceous elytral disc and sutural vittae, and black epipleura, elytral edge, and sutural margins.

Description: *Form* (Figure 4): Small and narrow; head quadrate; prothorax shorter than average for genus, cylindrical. Elytra flared in apical two-thirds, margins sinuate at beginning of flare at basal third.

Color: Shiny; appendages including mouthparts, abdomen, elytral apex and sutural vitta rufotestaceous; head, prothorax, mesosternum rufous; epipleura, elytral apical and sutural margin, metasternum black; elytral base metallic green.

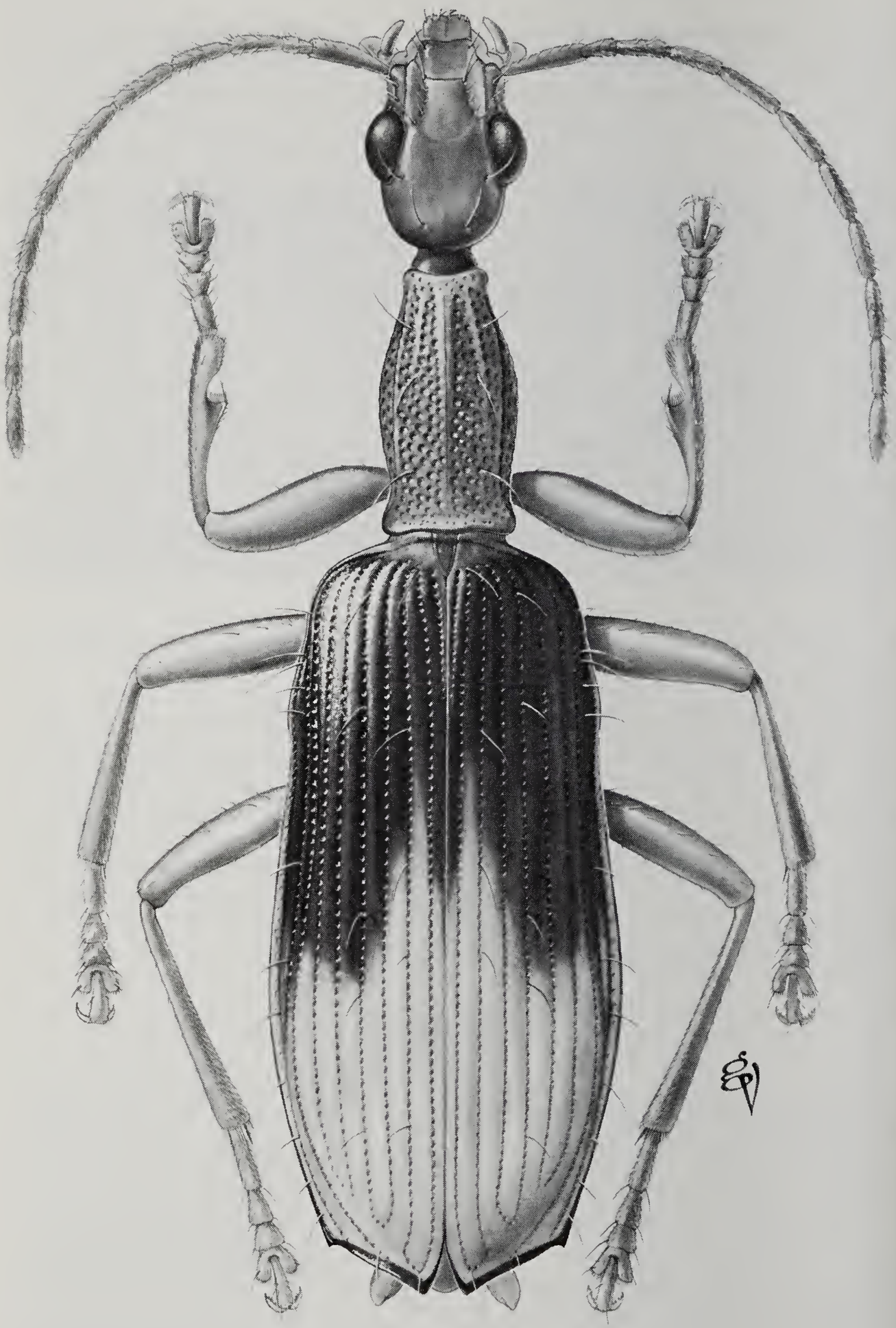

Figure 4. Habitus, dorsal aspect, of *Agra lavernae* Erwin, female holotype, Cerro Campana, Panama.

Head: Rectilinear, twice longer than wide (TLH 1.80 mm × TWH 0.94 mm), evenly depressed (TDH 0.68 mm); HE 1.24 mm; ID 0.94 mm; MFW 0.69 mm; LBE 1.33 mm; LFE 0.76 mm. Labrum quadrate, about same size as clypeus, entire; clypeus anteriorly emarginate; frons slightly sulcate at each side, carinate laterad to furrows, carina extends from apex to eye, curved around anterior supraorbital seta; mesad, occiput with pair of long setae; mentum with broad, rounded tooth.

Prothorax: Short and robust for genus, PL 1.91 mm, PW 1.01 mm; widest across basal margin, narrowest at apical margin, swollen medially, constricted near base, densely and coarsely punctate overall, some punctures with short setae. Pronotum with median central callous in apical third, flanked with paramedian carinae and paramedian setal rows, each probably normally with 3 setae (asymmetrically with 4 on right side in type). Proepipleura absent, in its place two parallel diffuse carinae, the ventral one with sharp carinule at basal tenth.

Elytra: Narrow basally, flared in apical two-thirds, margin sinuate, and 8th interval with slightly swollen callous at basal third, 6th and 7th intervals swollen at apical fourth; interneurs strongly and evenly punctate throughout their length to apex, punctulae separated by less than their own diameter, interneurs 2 and 4 each with 5 large setae, lateral channel with numerous setae; apical margin very slightly bisinuate, epipleuron sharply denticulate apically, mesal angle acute, trigonal, unisetose.

Abdomen: Tergum VI narrowly rounded apically; sternum VI medially notched, laterally angulate, with 4 long setae—2 at hind angles and 2 slightly mesad and anterior of hind angle; all sterna with scattered setae, 3 and 4 each with 1 pair of long setae, 5 with 3 pair long setae.

Legs: Normal for genus, all tibiae cylindrical; anterior femora not robust, not denticulate.

Microsculpture: Finely isodiamteric throughout.

Genitalia: Male unknown; female styli hemicylindrical, elongate, strongly sclerotized, with two stout spines apicodorsally.

Size: Standardized body length, 9.34 mm; width 3.04 mm; depth at hind coxa 1.55 mm.

Etymology: After years of searching, I finally discovered a beetle species elegant enough to name for my wife La Verne, in recognition of her contributions to the field of carabidology, namely computerized natural history, documentation of field data, collecting on three continents, editing and criticizing my contributions, lab work through the years, manuscript typing, and in general putting up with the aspirations of a beetle nut for so many years.

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